Importance of Coarse Woody Debris to Avian Communities in Loblolly Pine Forests

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Abstract: *To investigate the importance of standing (snags) and down coarse woody debris (DCWD) to bird communities in loblolly pine (*Pinus taeda*) forests, we compared breeding (1997-1999) and nonbreeding (1997-1998, 1998-1999) responses of birds among two coarse woody debris (CWD) removal and control treatments. In each of four blocks, we established four experimental units: (1) DCWD removed, (2) snags and DCWD removed, and (3) and (4) unmodified control plots. We quantified vegetation layers to determine their effects on the experimental outcome. Total breeding bird abundance, abundance of resident species, breeding bird diversity, breeding species richness, and abundance of Great Crested Flycatchers (*Myiarchus crinitus*) were reduced by the removal of DCWD and snags. Total woodpecker and Carolina Wren (*Thryothorus ludovicianus*) breeding territories were reduced by snag removal. Weak excavating and secondary cavity-nesting species, Neotropical migrants, and Eastern Towhees (*Pipilio erythrophthalmus*) had fewer breeding territories on plots where DCWD was removed. Red-headed Woodpeckers (*Melanerpes erythrocephalus*) and midstory and canopy-nesting species were at lowest densities on plots where all CWD had been removed. The CWD removal had no effect on the nonbreeding bird community. Most breeding and nonbreeding species used habitats with sparse midstory and well-developed understory, whereas sparse canopy cover and dense midstory were important to some nonbreeding species. Snag and DCWD retention, and practices that maintain a dense understory and sparse midstory and canopy, will create favorable breeding habitat for many bird species of loblolly pine forests.*

Importancia de Desechos Leñosos Gruesos para las Comunidades de Aves enBosques de *Pinus taeda*

Resumen: *Para investigar la importancia de troncos en pie (tocones) y de desechos leñosos gruesos caídos (DCWD) para las comunidades de aves en bosques de* Pinus taeda *comparamos las respuestas reproductivas (1997-1999) y no reproductivas (1997-1998, 1998-1999) de aves entre dos tratamientos de remoción y control de desechos leñosos gruesos (CWD). En cada uno de los cuatro bloques, establecimos cuatro unidades experimentales: (1) DCWD removidos, (2) tocones y DCWD removidos y (3) y (4) parcelas control no modificadas. Cuantificamos las capas de vegetación para determinar sus efectos sobre los resultados experimentales. La abundancia total de aves reproductoras, la abundancia de especies residentes, la densidad de aves reproductoras, la riqueza de especies en reproducción y la abundancia del papamoscas viajero (*Myiarchus crinitus*) estuvieron reducidas por la remoción de DCWD y tocones. El total de territorios de reproducción de pájaros carpinteros y del chivirín de Carolina (*Thryothorus ludovicianus*) fueron reducidos por la remoción de tocones. Especies cavadoras débiles y anidadoras secundarias de cavidades, migrantes neotropicales y el toquí pinto (*Pipilo erythrophthalmus*) tuvieron menos territorios de reproducción en parcelas donde los CWD caídos habían sido removidos. Los pájaros carpinteros cabeza roja (*Melanerpes erythrocephalus*) y especies de media altura y aquéllas que anidan en el dosel tuvieron sus densidades más bajas en parcelas donde todos los CWD fueron removidos. La remoción de CWD no tuvo efectos en las comunidades de aves que no se estaban reproduciendo. La mayoría de las especies en reproducción y las que no estaban en reproducción usaron hábitats con cobertura vegetal intermedia escasa y un sotobosque bien desarrollado, mientras que la cobertura de dosel escasa y la cobertura intermedia densa fueron importantes para algunas especies que no*

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estaban reproduciéndose. La retención de tocones y de DCWD y las prácticas que mantienen un sotobosque denso y una cobertura vegetal intermedia y de dosel escaso crearán hábitat favorable para la reproducción de muchas especies de aves de bosques del pino Pinus taeda.

Introduction

Coarse woody debris (CWD) has been positively associated with avian diversity and abundance (Scott 1979; Raphael & White 1984; Zarnowitz & Manuwal 1985; Schreiber & deCalesta 1992; Lanham & Guynn 1993). Snags (standing CWD) are a critical resource for many species of birds, especially those that use them for breeding and roosting. Previous studies suggest that breeding opportunities are often limited for cavity-nesting species because of lack of suitable nest sites (Raphael & White 1984; McComb et al. 1986; Schreiber & deCalesta 1992; Ohmann et al. 1994). Snags and down coarse woody debris (DCWD) are also used by other species for perching, foraging, and communicating (Davis 1983; Bull & Holthausen 1993; Lanham & Guynn 1993). Hamel (1992) cited 45 bird species that use snags and 9 species that use DCWD in the southeastern United States.

Forests of loblolly pine (*Pinus taeda*) dominate much of the landscape in the southeastern United States, covering 13.4 million ha (Schultz 1997). The species is one of the most intensely managed of southern trees because of its high yields at a relatively early age; as a result, rotation lengths are often <30 years. Snag removal, short harvest rotations, and intensive site preparation have drastically reduced the amount of CWD in southeastern forests and may therefore have had an adverse effect on the avian community (Scott 1979; Raphael & White 1984; Zarnowitz & Manuwal 1985).

A large-scale manipulative experiment in which CWD is completely removed is necessary to more fully understand the importance of CWD to bird communities. Many cavity-nesting birds are considered dependent on snags, but some of these species may adapt to alternative nest sites in the absence of snags rather than forfeit a breeding territory (Dingledine & Haufler 1983). Most studies only relate snag and bird abundance (McComb et al. 1986; Land et al. 1989; Ohmann et al. 1994). Few manipulative studies exist, and those that do either have no replication, do not consider DCWD, or do not include vegetation parameters that influence the bird community (Scott 1979; Dickson et al. 1983; Dingledine & Haufler 1983; Stribling et al. 1990). Lanham and Guynn (1993) emphasize the need for studies documenting the influence of CWD on bird-species occurrence and diversity in the southeastern United States. The objective of our study was to assess the importance of CWD in structuring the breeding and nonbreeding avian communities of southeastern pine forests through experimental removal of DCWD and all CWD.

Methods

Study Area

We conducted our research in loblolly pine forests on the U.S. Department of Energy's (DOE) Savannah River Site (SRS) on the upper coastal plain of South Carolina (lat. 33.3°N, long. 81.5°W). The SRS is an 80,200-ha tract designated a DOE National Environmental Research Park. It is dominated by upland loblolly and longleaf (*Pinus palustris*) pine forest.

Study Design

We used a randomized complete-block experimental design. Four blocks were selected based on the following stand criteria: loblolly pine (1) between 40 and 50 years of age, (2) ≥75 m from wetlands and major roads, and (3) large enough to encompass four 9.3-ha^2 experimental units. Our research sites were dominated by loblolly pine, with oak (*Quercus* sp.), longleaf pine, and slash pine (*P. elliottii*) occurring infrequently in the canopy. All blocks were on similar site types, but experimental units varied somewhat in density of understory, midstory, and canopy cover due to differences in past management. Midstory plant species included black cherry (*Prunus serotina*), mockernut hickory (*Caryo tomentosa*), wax myrtle (*Myrica cerifera*), American holly (*Ilex opaca*), and various species of oak (*Quercus* spp.). Common understory species consisted of American beautyberry (*Callicarpa americana*), plume grass (*Erianthus* sp.), and broomsedge (*Andropogon virginicus*). Invasive species such as kudzu (*Pueraria lobata*), Chinese privet (*Liqustrum sinese*), bicolor lespedeza (*Lespedeza bicolor*), muscadine (*Vitus rotundifolia*), and blackberry (*Rubus* spp.) were also present in some areas.

Within each block, three treatments were assigned randomly to 300 × 300 m areas within each of the four units. Treatments included (1) a control plot in which CWD remained unmodified, (2) a plot in which all DCWD >10 cm in diameter at midpoint was removed (hereafter, down removal), and (3) a plot where all snags and DCWD >10 cm in diameter at midpoint (for DCWD) or breast height (for standing CWD) were removed (hereafter, all removal). The fourth plot was designated for a treatment to be installed in the future for a subsequent study, but for our study it served as a second control. Initial treatments were made during July–August 1996, and subsequent annual removal of newly recruited CWD was conducted each January-March for the duration of the study. Removal was completed with light equipment (chain saws and four wheelers), and contractors were prohibited from using heavy machinery during removal. Disturbance to understory vegetation was minimal on removal plots, and no disturbance took place on control plots.

Experimental Outcomes

Five possible outcomes of the experiment were expected. In instances where no treatment differences were detected, CWD removal had no effect (outcome 1; control = down removal = all removal). Conversely, where territories and detections were successively decreased from control to all removal, both DCWD and snags influenced the result (outcome 2; control > down removal > all removal). When control treatments had more territories and detections than down and all removal (outcome 3; control > down removal = all removal), the reduction in the number of territories and detections was attributed to the removal of DCWD because no further decrease in territories and detections was evident with the removal of snags. When control and down-removal treatments had more territories than all removal (outcome 4; control = down removal > all removal), the difference was attributed to snags because all removal plots were the only plots with snags removed. In the final case in which only control and all removal plots differed (outcome 5; control = down removal, down removal = all removal, but control > all removal), we hypothesized that either DCWD or snags or a combination of the two were contributing factors.

Vegetation Sampling

We counted standing and DCWD stems in a 6-ha sampling unit in the center of each plot. Following the 1997 breeding season, we quantified three vegetative layers—understory, midstory, and canopy—with the zone-percent technique outlined by the Forest Inventory and Analysis Work Unit (1991). Understory vegetation was defined as occupying from 0 to 3 m, midstory as 3 to 14 m, and canopy as >14 m. We visualized an 11-m-diameter cylinder encompassing the entire vertical profile of each vegetation layer at 49 equally spaced grid points (50 × 50 m) on each plot. The percentage of foliage occupying the cylinder for deciduous (woody), pine, and other cover (vines and other herbaceous plants that persisted throughout the year) was then estimated for each vegetation layer. Means were calculated for each component of the vegetation layer on each plot for use in the statistical analysis (Appendix 1). Vegetation variables were used as covariates in the analyses for breeding and nonbreeding seasons to account for their effects on the experimental outcome.

Avian Sampling

The breeding-bird community was surveyed 5 May-3 July during the 1997-1999 breeding seasons by spot-mapping (Bibby et al. 1992; Ralph et al. 1993). Plots were traversed on transects that followed the 50-m grid system so that the routes passed within 50 m of any location on the plot. We recorded each bird heard or seen within the plot boundary (excluding fly-overs) and took care not to record the same individual more than once. Eight morning visits were made to each plot in 1997 and 1999. During 1998, two afternoon visits were added but did not affect species density or diversity estimates, so these visits were discontinued in 1999. Maps of all locations for each individual species present were generated to delineate the total number of territories for each species on the plot. We conducted nest searching on each plot to locate nests of woodpeckers because these species are not as easily mapped. Wide-ranging and nonterritorial species were excluded from the analysis (e.g., American Crow [*Corvus brachyrhynchos*], Fish Crow [*C. ossifragus*], Brown-headed Cowbird [*Molothrus ater*], and Wild Turkey). Morning surveys were begun 20 minutes after dawn and were completed 4 hours after sunrise; afternoon surveys were begun 3 hours before sunset and were concluded 0.5 hours before sunset. Both survey route and plot order were alternated to eliminate potential temporal or directional biases.

Nonbreeding birds were surveyed during the 1997-1998 and 1998-1999 nonbreeding seasons with methods outlined by Kolb (1965). Survey routes followed were the same as those during the breeding season, and all birds heard or seen on the plot were recorded. Species maps were not generated because nonbreeding territories were not evident for most species. Instead, total number of individuals of each species present was counted for each visit. Six visits were made to the plots during each nonbreeding season from December through February. Nonbreeding season surveys were started 20 minutes after dawn and were concluded by 1400 hours. Kolb (1965) suggests that nonbreeding bird activity is consistent throughout the day, so these surveys were conducted through midafternoon.

Statistical Analysis

The number of DCWD stems and snags for the experimental units was analyzed with a one-way analysis of variance (ANOVA) to determine the effectiveness of the removal treatments (PROC GLM; SAS Institute 1985). When no year-by-treatment interaction occurred, years were pooled in the analysis. When a significant treatment difference was found, a least-significant-difference (LSD) mean comparison test was conducted. Significance level was $\alpha \leq 0.05$ for all comparisons.

Overall abundance (all species combined), the Shannon-Weaver index of diversity (Shannon & Weaver 1949), and species richness were calculated and used as response variables. Abundance was defined as the mean number of territories per plot. All species with >35 territories during the breeding seasons or 100 detections during the nonbreeding seasons were analyzed individually in the same fashion. In addition, all species were placed in guilds according to their nest-site location observed on our sites during the breeding season (strong excavators, weak excavator/secondary cavity nesters, understory nesters, midstory/canopy nesters) and foraging preference during the nonbreeding season (bark gleaners, ground/understory gleaners, midstory/canopy gleaners). Data for guilds were analyzed to determine treatment effects on abundance in groups of species with similar nesting or foraging preferences. Abundance of resident and Neotropical migratory birds was also included in the analyses.

We used analysis of covariance (ANCOVA) to determine whether there was a significant treatment effect for each avian response variable tested (PROC MIXED; SAS Institute 1985). Because vegetation structural layers varied within blocks, ANCOVA including these nine variables—deciduous, pine, and other components of understory, midstory, and canopy—as covariates was necessary to eliminate their confounding effects on the treatments. Vegetation covariates were added in a stepwise fashion until the best model was found (covariates had to be significant at $\alpha < 0.05$ to be included). Significant vegetation parameters were assumed to be associated with the guilds or species being analyzed. Correlated covariates were not eliminated so that the more significant parameter could be identified in models. Simultaneous inclusion of correlated covariates did not occur, because interaction of these variables eliminated their significance. If a treatment effect was detected, an LSD test was conducted to ascertain differences in treatment types. If year-by-treatment interactions were significant, individual years were analyzed separately.

Table 1. Effectiveness of removal of snag and down coarse woody debris from experimental units.[a]

Treatment[b]	*Snags*	*DCWD*[c]
Control	8.5 (0.3) A	96.3 (4.1) A
Down removal	8.5 (0.4) A	9.3 (5.8) B
All removal	1.9 (0.4) B	6.0 (5.8) B
p[d]	0.0001	0.0001

[a] *Reported in mean stems per hectare, 1997–1999. Means (standard errors in parentheses) reported are least squares means used in pairwise comparisons.*
[b] *Down-removal plots have all down coarse woody debris removed; all-removal plots have both snags and down coarse woody debris removed.*
[c] *DCWD, down coarse woody debris.*
[d] *Generated from analysis of variance of treatment means; treatments not marked with a common letter were significantly different.*

Results

Breeding Season

Removal treatments were successful in eliminating CWD. Snags were more abundant on control and down-removal plots than on all-removal plots, whereas DCWD was lowest on down-removal and all-removal plots (Table 1).

We found 35 species and 1190 total territories over the three breeding seasons on the study site. The 12 most abundant species accounted for 80% of the total number of territories. The Pine Warbler (scientific names of birds are in appendices) was the most common breeding species, with 31 territories per 40 ha on control plots for the three seasons. Other species abundant on control plots included the Eastern Wood-Pewee, Carolina Wren, and Indigo Bunting, with 10, 9, and 8 territories per 40 ha, respectively (Appendix 2). Thirteen species had sufficient data to analyze individually (Table 2).

Red-bellied Woodpeckers, Tufted Titmice, Brown-headed Nuthatches, Carolina Chickadees, understory nesters, Indigo Buntings, Northern Cardinals, Pine Warblers, Eastern Wood-Pewees, and Summer Tanagers (1997, 1999) were not affected by CWD removal (outcome 1). Overall abundance, diversity, richness, residents, and Great Crested Flycatchers were negatively affected ($p < 0.05$) by both DCWD and snag removal (outcome 2). Neotropical migrants, weak excavator/secondary cavity nesters, Eastern Towhees, and Eastern Wood-Pewees (1999) were reduced by DCWD removal (outcome 3). Strong excavators (1997, 1998, 1999), Carolina Wrens, and Eastern Wood-Pewees (1998) were negatively affected by snag removal (outcome 4). Red-headed Woodpeckers and midstory/canopy nesters were negatively affected by DCWD and snag removal (outcome 5). Summer Tanagers (1998) were positively affected by DCWD removal treatments.

Pine and deciduous midstory most commonly influenced the breeding-bird community. In 15 of 22 groups or species analyzed, at least one measure of midstory negatively influenced abundance or diversity (Table 2). Understory influenced only six of the instances, and all but one of these associations was positive (Table 2). Canopy had a negative effect on only one of the tests (Table 2).

Nonbreeding Season

We detected 6606 birds of 37 species during two nonbreeding seasons (Appendix 3). The Yellow-rumped Warbler (*Dendroica coronata*) was the most abundant species and accounted for over 50% of the total number

Table 2. Mean (SE) breeding-bird territories per experimental unit on each treatment and vegetation covariate, with effects on the group or bird species, 1997–1999.

		Treatment[a]				*Covariate*	
Grouping		*control*	*down removal*	*all removal*	p	*parameter*[b]	p
Total territories		31.1 (2.0) A	20.7 (2.1) B	16.3 (2.2) C	0.006	PM(−)	<0.001
						DM(−)	0.007
						TOTU(+)	0.014
Shannon-Weaver		2.99 (0.15) A	2.40 (0.16) B	2.11 (0.16) C	0.006	PM(−)	<0.001
						DM(−)	0.004
Species richness		19.9 (1.6) A	13.4 (1.6) B	10.8 (1.6) C	0.002	PM(−)	<0.001
						DM(−)	<0.001
Residents		22.3 (1.2) A	15.9 (1.3) B	11.2 (1.3) C	0.004	PM(−)	<0.001
						DM(−)	0.032
						OM(−)	0.025
Neotropical migrants		9.4 (1.3) A	4.7 (1.3) B	3.9 (1.3) B	0.016	DM(−)	0.006
						PM(−)	0.006
strong excavators	1997	4.1 (0.5) A	3.6 (0.5) A	1.9 (0.5) B	0.033	none	
	1998	4.9 (0.6) A	3.4 (0.7) A	0.8 (0.7) B	0.009	none	
	1999	3.1 (0.5) A	3.4 (0.6) A	0.9 (0.6) B	0.026	none	
Red-headed Woodpecker		1.6 (0.3) AB	0.8 (0.3) AB	0.2 (0.3) B	0.023	none	
Red-bellied Woodpecker		0.9 (0.2) A	1.2 (0.2) A	0.7 (0.2) A	0.084	TOTM(−)	0.016
weak excavator/secondary cavity nesters		4.7 (0.4) A	2.2 (0.5) B	1.9 (0.5) B	0.037	PM(−)	0.002
						DM(−)	0.017
						OM(−)	0.030
Great Crested Flycatcher		1.5 (0.2) A	0.4 (0.2) B	0.2 (0.2) C	0.02	PM(−)	0.031
						DM(−)	0.006
Tufted Titmouse		1.1 (0.2) A	0.9 (0.2) A	1.2 (0.2) A	0.662	DU(+)	0.004
						PU(+)	0.009
Brown-headed Nuthatch		0.9 (0.1) A	0.7 (0.2) A	0.5 (0.2) A	0.077	none	
Carolina Chickadee		0.9 (0.1) A	0.3 (0.2) A	0.3 (0.2) A	0.121	DM(−)	0.028
						PM(−)	0.038
						OM(−)	0.024
Understory nesters		8.1 (0.9) A	6.2 (1.0) A	5.1 (1.0) A	0.155	OU(+)	<0.001
						PM(−)	0.005
						OM(−)	0.008
Carolina Wren		2.8 (0.3) A	1.9 (0.3) A	1.0 (0.3) B	0.006	DM(−)	<0.001
						PM(−)	<0.001
						OM(−)	0.002
Indigo Bunting		1.5 (0.2) A	1.0 (0.2) A	1.1 (0.3) A	0.292	OU(+)	<0.001
						DC(−)	0.016
Eastern Towhee		1.9 (0.3) A	0.1 (0.3) B	0.6 (0.3) B	0.042	PU(+)	<0.001
						OU(+)	0.003
						PM(−)	<0.001
						DM(−)	0.008
Northern Cardinal		1.1 (0.2) A	0.8 (0.2) A	0.4 (0.2) A	0.101	PM(−)	0.017
						OM(−)	0.018
Midstory/canopy nesters		12.4 (0.4) A	11.4 (0.6) AB	10.1 (0.6) B	0.049	PM(−)	0.005
Pine Warbler		7.3 (0.3) A	6.5 (0.5) A	5.7 (0.5) A	0.088	None	
Eastern Wood-Pewee	1997	1.8 (0.2) A	2.4 (0.3) A	2.5 (0.3) A	0.333	DM(−)	0.017
	1998	2.3 (0.3) A	2.5 (0.3) A	1.0 (0.3) B	0.018	none	
	1999	1.9 (0.3) A	0.9 (0.4) B	1.3 (0.4) AB	0.047	none	
Summer Tanager	1997	1.3 (0.2) A	1.7 (0.3) A	1.6 (0.2) A	0.081	PU(−)	0.031
	1998	1.3 (0.1) A	1.9 (0.2) B	1.0 (0.2) A	0.053	none	
	1999	1.1 (0.2) A	0.8 (0.3) A	1.3 (0.3) A	0.570	none	

[a] *Down removal plots have all down coarse woody debris removed; all removal have both snags and down coarse woody debris removed. Means followed by the same letter in a row do not differ significantly. Means and standard errors reported are least squares means of territories per plot used in pairwise comparisons. Treatments not marked with a common letter were significantly different.*

[b] *Abbreviations: PU, pine understory; DU, deciduous understory; OU, other understory; TOTU, total understory; PM, pine midstory; DM, deciduous midstory; OM, other midstory; TOTM, total midstory; PC, pine canopy; DC, deciduous canopy; TOTC, total canopy. Sign indicates nature of relationship.*

Table 3. Mean (SE) detections of nonbreeding birds per experimental unit for each treatment, including vegetation covariates affecting bird groups or species.

	Treatments[a]				Covariates	
Grouping	*control*	*down removal*	*all removal*	p	*parameter*[b]	p
Total detections	35.2 (5.8)	41.9 (13.4)	25.4 (8.2)	0.57	none	
Shannon-Weaver	1.80 (0.15)	1.80 (0.28)	1.72 (0.2)	0.09	DM(−)	0.008
					PC(−)	0.02
Species richness	16.6 (1.3)	15.6 (1.4)	13.8 (1.1)	0.46	TOTU(+)	0.002
Residents	12.4 (2.4)	9.9 (1.8)	7.4 (1.1)	0.28	TOTC(−)	0.0001
Nearctic migrants	22.8 (4.2)	32.1 (14.2)	18.0 (8.5)	0.76	DC(−)	0.01
					TOTU(+)	0.047
Bark gleaners	1.9 (0.2)	1.6 (0.2)	1.6 (0.4)	0.63	none	
Brown-headed Nuthatch	0.8 (0.1)	0.6 (0.2)	0.5 (0.2)	0.51	TOTC(−)	0.02
Red-bellied Woodpecker	0.6 (0.1)	0.5 (0.1)	0.6 (0.2)	0.16	OU(+)	0.02
					DM(+)	0.04
Ground/understory gleaners	9.0 (3.4)	6.7 (2.2)	3.2 (1.0)	0.90	PC(−)	0.003
					DC(−)	0.02
Chipping Sparrow	3.7 (1.6)	2.0 (1.2)	1.1 (0.8)	0.67	PC(−)	0.01
					DC(−)	0.01
Dark-eyed Junco	2.0 (0.6)	1.9 (1.2)	0.1 (0.1)	0.14	none	
Carolina Wren	0.6 (0.1)	0.8 (0.2)	0.2 (0.1)	0.15	PM(−)	0.01
					DM(−)	0.01
					TOTU(+)	0.01
Mourning Dove	0.6 (0.3)	0.6 (0.4)	0.4 (0.2)	0.98	none	
Midstory/canopy gleaners	24.2 (5.9)	33.5 (14.1)	20.6 (8.5)	0.64	DC(−)	0.01
					OU(+)	<0.05
Yellow-rumped Warbler	16.3 (3.9)	25.3 (14.2)	13.3 (8.8)	0.71	DC(−)	0.0001
					OU(+)	0.04
Pine Warbler	3.5 (0.4)	3.2 (0.4)	3.1 (0.5)	0.24	PC(−)	0.009
Ruby-crowned Kinglet	1.4 (0.2)	2.9 (0.7)	2.0 (0.6)	0.35	TOTM(+)	0.02
Red-winged Blackbird	1.2 (0.6)	0.0 (0.0)	0.0 (0.0)	0.13	none	
Golden-crowned Kinglet	0.3 (0.1)	0.7 (0.3)	0.8 (0.3)	0.42	OM(+)	<0.05
Carolina Chickadee	0.5 (0.1)	0.6 (0.2)	0.4 (0.1)	0.99	none	

[a]*Down-removal plots have all down coarse woody debris removed; all-removal plots have both snags and down coarse woody debris removed. Mean and standard error are of the number of detections per visit to each plot; log of the total number of detections was used in the analysis of covariance. Treatments not marked with a common letter were significantly different.*
[b]*Parameter abbreviations defined in Table 2. Sign indicates nature of relationship.*

of detections. Twelve species represented 91% of the birds detected during the nonbreeding season.

No species grouping or individual species exhibited significant treatment effects during the nonbreeding season (Table 3), but canopy cover was inversely proportional to abundance or diversity for nearly half of the groupings, whereas understory had a positive association in six instances (Table 3). Midstory elicited both positive and negative responses but affected only four groupings (Table 3).

Discussion

Breeding Season

Snag and DCWD removal reduced overall abundance and species diversity and richness of the breeding bird community in loblolly pine forests. This effect was not limited to cavity-nesting birds: Carolina Wrens, Eastern Towhees, Eastern Wood-Pewees, and Summer Tanagers also were affected. Complete removal of CWD diminished breeding-bird abundance by nearly 50% and richness by 45%. With increasing disturbance to the habitat (i.e., control to down removal to all removal), values declined, indicating that DCWD and snags augmented abundance, diversity, and richness. Dickson et al. (1983) found that hardwood snag retention in Texas clearcuts increased species diversity. Other studies have either not tested for community response to reduction in snag density or have found no difference in species other than cavity nesters (Scott 1979; Dingledine & Haufler 1983; Schreiber & deCalesta 1992), and studies indicating a correlation between avian communities and DCWD are lacking.

Snag removal had a drastic effect on many cavity-nesting species. We found that overall woodpecker abundance was intimately linked with the presence of snags. Woodpeckers are associated positively with snag density in various habitats (Dickson et al. 1983; Raphael & White 1984; Zarnowitz & Manuwal 1985; Schreiber & deCalesta 1992), although studies documenting this relationship in the southeast are lacking. Land et al. (1989) failed to find a correlation between snag density and cavity-nesting species in slash-pine plantations of Florida. Red-headed Woodpeckers nested exclusively in pine snags on our site, so we believe that the difference between control and all-removal treatments was due largely to the elimination of snags as a breeding resource. Great Crested Flycatchers, a secondary cavity-nesting species, were also affected by snag removal. Because Great Crested Flycatchers may not compete well with larger species such as Red-headed Woodpeckers (Lanyon 1997), the removal of snags eliminates a significant portion of their potential nest sites, thus limiting their abundance. Snags may also be important as a foraging resource to some cavity-nesting species. In a concurrent study on our site, Horn (2000) found that arthropod abundance was reduced on all removal plots, so a reduction in prey abundance associated with snags may also affect cavity nesters. Several other cavity-nesting species were not affected by snag removal. Red-bellied Woodpeckers, Brown-headed Nuthatches, Tufted Titmice, and Carolina Chickadees used alternative nest sites on all removal plots, including dead limbs, decomposing stumps, and natural crevasses. Thus, these species may not exclusively use snags as a nesting substrate, relaxing their dependence on the resource.

Treatment differences varied between years for strong excavators (Table 2), with the overall trend remaining the same. In 1997, the first year after removal, complete removal reduced abundance by only 54%, whereas in 1998 and 1999 abundance was reduced by over 70%. The most abundant woodpecker, the Red-Headed woodpecker, is a migratory species not present on the site during the nonbreeding season which often returns to the same breeding territory each year (Ingold 1991). The Red-headed Woodpeckers found the habitat drastically modified upon their arrival to breed during the 1997 season and may not have been able to reestablish new territories with suitable nest sites. By 1998 and 1999, however, the birds had suitable opportunity to acquire breeding sites elsewhere, perhaps packing into the surrounding habitats, because more woodpecker nests were found on control and down-removal plots during 1998 and 1999 than in 1997 (S.M.L., unpublished data).

Coarse woody debris was an important structural characteristic for several open-nesting species. The Eastern Wood-Pewee, a flycatching species, was affected by snag removal in 1998. Balda (1969) reported that Western Wood-Pewees (*Contopus sordidulus*) use snags for hunting and singing in Arizona. Other open-nesting species, including Scarlet Tanagers (*Piranga olivacea*) and American Robins (*Turdus migratorius*), have been reduced by snag removal (Scott 1979; Dingledine & Haufler 1983). Despite the fact that the Carolina Wren was never found nesting in cavities associated with CWD, the species was most abundant on plots containing snags. Carolina Wrens forage predominately on arthropod prey, with a large portion of their diet consisting of hemipterans (Haggerty & Morton 1995). Horn (2000) found hemipterans reduced on all removal plots, so food availability may be the limiting factor on all removal plots for Carolina Wrens and other open-nesting species. Down CWD removal reduced the abundance of weak, excavator/secondary cavity nesters, Neotropical migrants, and resident groups on our site. Down CWD harbors insect prey and provides additional structure for birds in forests (Shackelford & Conner 1997; Hagan & Grove 1999). Great Crested Flycatchers and Eastern Towhees also declined as a result of DCWD removal. Down CWD may provide perches and increase arthropod abundance for flycatchers and may serve as nesting substrate for towhees on our site.

Breeding birds used habitats with reduced midstory and well-developed understory. Although our measure of understory included growth to 3 m, the majority of the understory vegetation recorded was herbaceous growth occurring below 2 m, which is typical of fire-maintained southern pine ecosystems. Species of these ecosystems prefer more-open stands, possibly facilitating foraging, flight, and location of predators (Shackelford & Conner 1997). Our results are consistent with results from studies of Red-cockaded Woodpeckers (*Picoides borealis*), indicating that midstory may be detrimental to birds of southern pine ecosystems. Fire historically played an important role in southern pine ecosystems and limited the amount of midstory in these forests. Wilson et al. (1995) found that burned and thinned stands have greater bird abundance than unburned and unthinned pine-hardwood stands in Arkansas. Understory nesters were virtually eliminated following fire exclusion in pine forests of Florida because the developing midstory layer reduced the amount of understory cover available for nesting and foraging (Engstrom et al. 1984). Reduced understory density and diversity may decrease arthropod abundance for the avian community. On our site, reduced understory negatively affected the Indigo Bunting and Eastern Towhee, both declining species in the region (Sauer et al. 1999).

Nonbreeding Season

Coarse woody debris apparently was not an important feature of the habitat for nonbreeding birds. However, experimental units may not have been of sufficient size to detect differences in nonbreeding bird abundance between CWD treatments. Nonbreeding species are not restricted spatially to territories as in the breeding season, and they roam over a much larger area. Woodpeckers, which use cavities for roosting during the nonbreeding season, were often seen foraging on all removal plots far from the nearest snag during the nonbreeding season.

Appendix 2. Mean (SE) breeding territories per 40 ha (1997–1999) for each coarse woody debris treatment.[a]

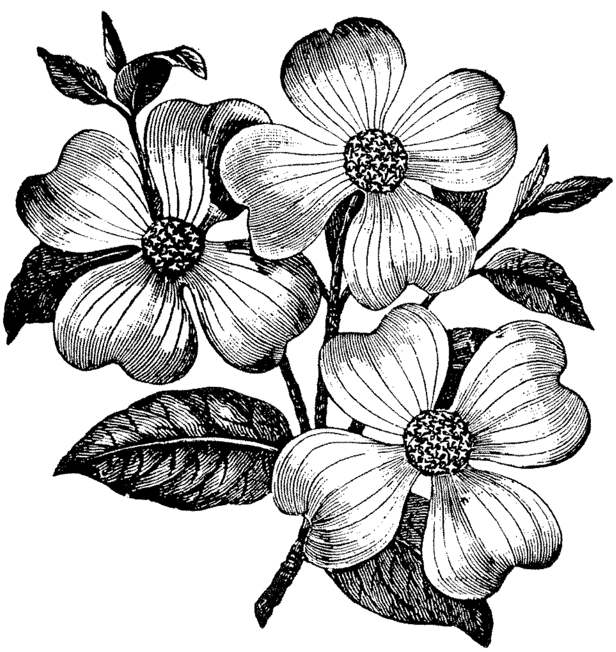
Group/species	*Control*	*Down removal*	*All removal*
Strong excavators	17.2 (1.3)	14.9 (1.4)	5.0 (1.2)
Red-bellied Woodpecker (*Melanerpes carolinus*)[b]	4.7 (0.4)	4.8 (0.5)	2.2 (0.7)
Red-headed Woodpecker (*Melanerpes erythrocephalus*)	6.8 (0.8)	3.6 (0.4)	0.7 (0.4)
Downy Woodpecker (*Picoides pubescens*)[b]	1.7 (0.4)	2.7 (0.6)	1.3 (0.4)
Northern Flicker (*Colaptes auratus*)[b]	2.5 (0.3)	2.5 (0.6)	0.4 (0.2)
Pileated Woodpecker (*Dryocopus pileatus*)[b]	1.0 (0.5)	0.9 (0.4)	0.5 (0.3)
Hairy Woodpecker (*Picoides villosus*)[b]	0.5 (0.2)	0.4 (0.2)	0.0 (0.0)
Weak excavators/secondary cavity nesters	16.2 (1.2)	14.7 (1.5)	10.9 (1.7)
Tufted Titmouse (*Baeolophus bicolor*)[b]	4.6 (0.7)	5.0 (0.9)	3.9 (0.6)
Great Crested Flycatcher (*Myiarchus crinitus*)[c]	4.7 (0.5)	3.6 (0.8)	2.5 (0.5)
Brown-headed Nuthatch (*Sitta pusilla*)[b]	3.8 (0.3)	3.0 (0.6)	2.2 (0.6)
Carolina Chickadee (*Poecile carolinensis*)[b]	2.7 (0.4)	2.7 (0.5)	2.3 (0.6)
Eastern Bluebird (*Sialia sialis*)[b]	0.5 (0.4)	0.0 (0.0)	0.0 (0.0)
Wood Duck (*Aix sponsa*)	0.0 (0.0)	0.4 (0.4)	0.0 (0.0)
Understory nesters	33.8 (3.6)	29.9 (4.0)	17.0 (2.6)
Carolina Wren (*Thryothorus ludovicianus*)[b]	9.1 (0.6)	12.0 (0.9)	6.3 (1.2)
Indigo Bunting (*Passerina cyanea*)[c]	7.5 (1.1)	4.1 (1.0)	2.9 (0.8)
Eastern Towhee (*Pipilo erythrophthalmus*)[b]	5.9 (0.8)	4.7 (1.4)	2.7 (0.7)
Northern Cardinal (*Cardinalis cardinalis*)[b]	4.7 (0.6)	4.5 (0.9)	1.3 (0.6)
Blue Grosbeak (*Guiraca caerulea*)[c]	0.5 (0.3)	1.8 (0.6)	1.3 (0.5)
Prairie Warbler (*Dendroica discolor*)[c]	2.0 (0.7)	0.7 (0.5)	0.5 (0.4)
Bachman's Sparrow (*Aimophila aestivalis*)[b]	1.5 (0.5)	0.4 (0.4)	0.9 (0.5)
Brown Thrasher (*Toxostoma rufum*)[b]	1.4 (0.4)	1.1 (0.6)	0.2 (0.2)
Chipping Sparrow (*Spizella passerina*)[b]	0.7 (0.4)	0.7 (0.5)	1.1 (0.6)
Northern Bobwhite (*Colinus virginianus*)[b]	0.2 (0.1)	0.0 (0.0)	0.0 (0.0)
Yellow-breasted Chat (*Icteria virens*)[c]	0.2 (0.2)	0.0 (0.0)	0.0 (0.0)
White-eyed Vireo (*Vireo griseus*)[c]	0.1 (0.1)	0.0 (0.0)	0.0 (0.0)
Midstory/canopy nesters	54.0 (1.9)	49.6 (2.3)	41.8 (2.9)
Pine Warbler (*Dendroica pinus*)[b]	31.2 (1.4)	27.8 (1.8)	24.6 (1.6)
Eastern Wood-Pewee (*Contopus virens*)[c]	9.9 (0.5)	7.3 (1.1)	5.6 (1.2)
Summer Tanager (*Piranga rubra*)[c]	5.2 (0.5)	5.9 (0.8)	5.7 (0.6)
Blue Jay (*Cyanocitta cristata*)[b]	3.0 (0.4)	3.6 (0.4)	1.4 (0.6)
Red-eyed Vireo (*Vireo olivaceus*)[c]	0.7 (0.3)	2.8 (0.7)	2.3 (0.6)
Yellow-billed Cuckoo (*Coccyzus americanus*)[c]	0.9 (0.3)	1.3 (0.5)	0.9 (0.4)
Yellow-throated Vireo (*Vireo flavifrons*)[c]	1.3 (0.4)	0.0 (0.0)	0.7 (0.4)
Mourning Dove (*Zenaida macroura*)[b]	0.9 (0.3)	0.5 (0.4)	0.2 (0.2)
Blue-gray Gnatcatcher (*Polioptila caerulea*)[c]	0.7 (0.3)	0.4 (0.2)	0.0 (0.0)
Acadian Flycatcher (*Empidonax virescens*)[c]	0.0 (0.0)	0.0 (0.0)	0.4 (0.4)
American Goldfinch (*Carduelis tristis*)[b]	0.2 (0.2)	0.0 (0.0)	0.0 (0.0)

[a] *Down-removal plots have all down coarse woody debris removed; all-removal plots have both snags and down coarse woody debris removed.*
[b] *Resident species.*
[c] *Neotropical migrant.*

Appendix 3. Mean (SE) number of nonbreeding detections per 40 ha (1997–1998 and 1998–1999) for each coarse woody debris treatment.

Group/species[a]	*Control*	*Down removal*	*All removal*
Bark gleaners	8.0 (0.9)	7.0 (0.8)	6.9 (1.7)
Brown-headed Nuthatch (*Sitta pusilla*)[b]	3.2 (0.6)	2.4 (0.8)	2.0 (1.0)
Red-bellied Woodpecker (*Melanerpes carolinus*)[b]	2.6 (0.4)	2.0 (0.4)	2.7 (0.7)
Downy Woodpecker (*Picoides pubescens*)[b]	1.0 (0.2)	1.1 (0.3)	1.2 (0.2)
Yellow-bellied Sapsucker (*Sphyrapicus varius*)[c]	0.5 (0.1)	0.4 (0.2)	0.5 (0.3)
Pileated Woodpecker (*Dryocopus pileatus*)[b]	0.4 (0.1)	0.8 (0.3)	0.2 (0.2)
Hairy Woodpecker (*Picoides villosus*)[b]	0.3 (0.2)	0.4 (0.2)	0.1 (0.1)
Ground/shrub gleaners	39.1 (10.3)	29.5 (9.2)	13.8 (4.3)
Chipping Sparrow (*Spizella passerina*)[b]	15.8 (6.7)	8.4 (5.2)	4.8 (3.5)
Dark-eyed Junco (*Junco hyemalis*)[c]	8.4 (2.6)	8.2 (5.1)	0.4 (0.4)
Carolina Wren (*Thryothors ludovicianus*)[a]	2.7 (0.5)	3.6 (0.7)	1.0 (0.3)
Mourning Dove (*Zenaida macroura*)[a]	2.6 (1.3)	2.6 (1.7)	1.9 (1.0)
Fox Sparrow (*Passerella iliaca*)[c]	1.5 (0.9)	1.5 (1.1)	2.7 (2.7)
Hermit Thrush (*Catharus guttatus*)[c]	0.9 (0.2)	1.9 (0.7)	1.5 (0.5)
Eastern Towhee (*Pipilo erythrophthalmus*)[b]	1.4 (0.9)	0.3 (0.3)	0.1 (0.1)
Northern Bobwhite (*Colinus virginianus*)[b]	1.0 (1.0)	1.1 (1.1)	0.0 (0.0)
Northern Flicker (*Colaptes auratus*)[b]	1.0 (0.3)	0.4 (0.2)	0.4 (0.3)
American Robin (*Turdus migratorius*)[c]	1.1 (0.9)	0.1 (0.1)	0.1 (0.1)
Northern Cardinal (*Cardinalis cardinalis*)[b]	0.7 (0.4)	0.6 (0.3)	0.2 (0.1)
Wild Turkey (*Meleagris gallopavo*)[b]	0.9 (0.8)	0.0 (0.0)	0.0 (0.0)
Eastern Bluebird (*Sialia sialis*)[b]	0.3 (0.2)	0.2 (0.2)	0.3 (0.3)
Midstory/canopy gleaners	98.7 (17.6)	144.0 (60.9)	88.6 (36.5)
Yellow-rumped Warbler (*Dendroica coronata*)[c]	70.2 (16.8)	108.8 (61.1)	57.3 (38.0)
Pine Warbler (*Dendroica pinus*)[b]	15.1 (1.5)	13.9 (1.6)	13.2 (2.2)
Ruby-crowned Kinglet (*Regulus calendula*)[c]	6.1 (1.0)	12.6 (2.9)	8.4 (2.5)
Red-winged Blackbird (*Agelaius phoeniceus*)[c]	5.3 (2.7)	0.1 (0.1)	0.0 (0.0)
Golden-crowned Kinglet (*Regulus satrapa*)[b]	1.4 (0.4)	2.9 (1.5)	3.4 (1.4)
Carolina Chickadee (*Poecile carolinensis*)[b]	2.3 (0.5)	2.5 (0.7)	1.8 (0.4)
Eastern Phoebe (*Sayornis phoebe*)[c]	1.7 (0.3)	1.5 (0.4)	1.7 (0.3)
Tufted Titmouse (*Baeolophus bicolor*)[b]	1.3 (0.3)	1.5 (0.5)	1.4 (0.4)
Blue-headed Vireo (*Vireo solitarius*)[c]	0.5 (0.2)	0.1 (0.1)	1.0 (0.4)

[a]*Down-removal plots have all down coarse woody debris removed; all-removal plots have both snags and down coarse woody debris removed.*
[b]*Resident species.*
[c]*Nonbreeding species.*



Capercaillie (*Tetrao urogallus*) and Avian Biodiversity: Testing the Umbrella-Species Concept

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Abstract: *Because of limited resources, biodiversity conservation practice is often reduced to measures directed at single species in the hope that this will simultaneously benefit other species in the same community. Such "umbrella species" should therefore have habitat requirements that are similar to those of the other species, whereas their spatial needs should be more extensive. The umbrella-species concept is often applied in management yet rarely tested beforehand. The Capercaillie (*Tetrao urogallus*) is a large forest grouse that is declining over much of its range in Central Europe. It is considered a good example of an umbrella species and is now widely receiving attention from forestry managers. We tested its usefulness as an umbrella species in the Swiss Prealps by analyzing relationships between Capercaillie occurrence and avian biodiversity and asked whether both were associated with the same habitat-structure parameters. Study plots with Capercaillie did not hold significantly higher bird diversity than plots without the grouse. However, the species richness and abundance of birds that are more or less restricted to subalpine forests (mountain birds) and that at the same time are on the red list was considerably higher in Capercaillie plots than in those without Capercaillie. Both Capercaillie and mountain birds responded positively to forest structure characterized by intermediate openness, multistoried tree layer, presence of ecotonal conditions, and abundant cover of ericaceous shrubs. Capercaillie may therefore be a useful umbrella species, at least for that part of avian biodiversity of conservation interest.*

Capercaillie (*Tetrao urogallus*) y Biodiversidad de Aves: Probando el Concepto de Especie Sombrilla

Resumen: *Debido a la escasez de recursos, la práctica de la biología de la conservación se reduce a menudo a medidas dirigidas a una sola especie con la esperanza de que esto beneficiará simultáneamente a otras especies de la misma comunidad. Por lo tanto, esas "especies sombrilla" deben tener requerimientos de hábitat similares a los de las otras especies, mientras que sus necesidades espaciales deben ser mayores. El concepto de especie sombrilla se aplica en manejo a menudo, sin embargo rara vez es probado antes. El Capercaillie (*Tetrao urogallus*) es un urogallo que esta declinando en gran parte de su rango en Europa Central. Es considerado un buen ejemplo de una especie sombrilla y esta recibiendo considerable atención de los manejadores de bosques. Probamos su utilidad como especie sombrilla en los Prealpes Suizos analizando relaciones entre la ocurrencia de Capercaillie y la biodiversidad de aves y preguntando si ambos estaban asociados con los mismos parámetros de la estructura del hábitat. Las parcelas de estudio con Capercaillie no presentaron significativamente mayor biodiversidad que las parcelas sin urogallos. Sin embargo, la riqueza y abundancia de especies de aves que están más o menos restringidas a bosques subalpinos (aves de montaña) y, al mismo tiempo, están en la Lista Roja fue considerablemente mayor en parcelas con Capercaillie que en parcelas sin urogallos. Tanto Capercaillie como aves de montaña respondieron positivamente a la estructura del bosque caracterizada por apertura intermedia, estrato arbóreo multiestratificado, presencia de condiciones ecotonales y abundante cobertura de arbustos ericáceos. Por tanto, Capercaillie puede ser una especie sombrilla útil, por lo menos para la biodiversidad de aves de interés para la conservación.*

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